

THE PHYLOGENETIC SYSTEM OF THE STENOGASTRINAE (HYMENOPTERA: VESPIDAE)

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Abstract.—The phylogenetic relationships of the genera of Stenogastrinae are investigated using cladistic methods. The cladogram here proposed is: *Liostenogaster* + ((*Eustenogaster* + *Stenogaster*) + (*Anischnogaster* + (*Metischnogaster* + (*Holischnogaster* + *Parischnogaster*))))). *Holischnogaster* is newly synonymized with *Parischnogaster*.

The Stenogastrinae, members of which might be called hover wasps, is a group of great current interest. They are thought to exhibit considerable diversity in social behavior, ranging from species which have been termed solitary (e.g., Williams, 1919), to primitively social species (lacking reproductive castes; cf. West-Eberhard, 1978), to eusocial species (Yoshikawa et al., 1969; Hansell et al., 1982; Turillazzi and Pardi, 1982). Additionally, they occupy a phylogenetically intermediate position between the solitary Eumeninae and the eusocial Polistinae and Vespinae (Carpenter, 1981). The group is thus of particular importance in the study of the evolution of social behavior in wasps. Reflecting this, the past decade has seen more behavioral studies on this subfamily than any time previously, as especially evidenced in the publications of Hansell, Turillazzi, and coworkers. However, much discussion of the evolutionary significance of the behavioral features treated in these works is confused, because of the lack of a phylogenetic perspective. The implications of the cladistic analysis of vespid subfamilies by Carpenter (1981) have not been properly appreciated, and no phylogenetic treatment of taxa below the subfamily level has been available. In the present work I address both of these issues. The conclusions of Carpenter (1981) are reiterated and extended, and a cladistic analysis of stenogastrine genera is presented. The results provide a point of departure for future evolutionary investigations of these wasps.

SUBFAMILY PLACEMENT

Carpenter (1981) provided the first cladistic analysis of any vespid taxon. The results of that study for subfamily relationships are shown in Figure 1. Stenogastrinae is the sister-group of Polistinae + Vespinae; Eumeninae is the sister-group of this component. This conclusion accords with traditional treatments such as Saussure (1852-1858) and Richards (1962), but is contrary to the views expressed by Richards (1971), Spradbery (1975) and van der Vecht (1977a). Richards (1971:486) observed that stenogastrines "are very different from other social wasps" in having a long pointed clypeus, long narrow mandibles and placement of the pronotal lobe halfway between the tegula and midcoxa. He stated that they "might even have evolved independently from some *Eumenes*-like, solitary ancestor." Spradbery presented a table comparing 17 "biological" characters for these four subfamilies. Finding that

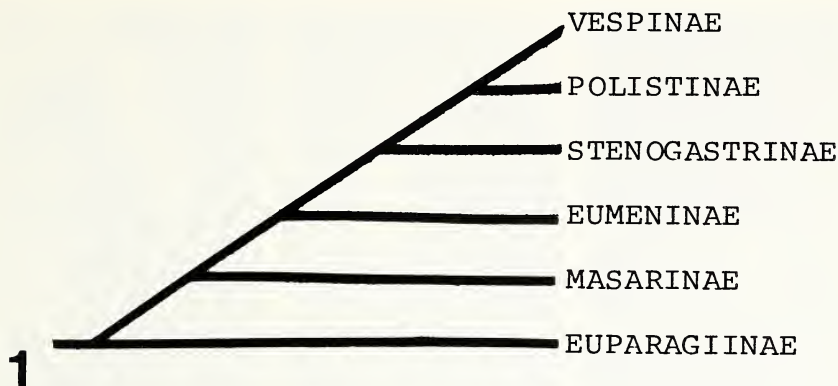


Fig. 1. Cladogram of vespid subfamilies after Carpenter (1981).

stenogastrines were in some respects intermediate between eumenines and the other social wasps, but also possessed of some unique features, he concluded that they “originated from an early vespoid ancestor,” by which he meant that they were not closely related to other extant social wasps. This is shown by his statement “it would be unwise to look to the Stenogastrinae for examples illustrating intermediate steps in the achievement of social organization by higher Vespidae.” These conclusions do not follow. Neither Richards nor Spradbery presented any evidence to indicate that hover wasps and other social wasps are not closely related phylogenetically. Their interpretations are based on Stenogastrinae being “different,” that is possessing autapomorphies, as I have pointed out before (Carpenter, 1981). Autapomorphies (unique derived features) are irrelevant to phylogenetic placement—they merely demonstrate that the taxa possessing them are monophyletic (Hennig, 1966). Further, as will be shown, in the features listed by Spradbery in which the Stenogastrinae are intermediate between eumenines and higher social wasps, the similarity to the higher social wasps is derived while the similarity to the eumenines is primitive. Only derived similarity—synapomorphy—indicates close phylogenetic relationship (Hennig, 1966).

Van der Vecht (1977a) made a similar logical error. He listed eight characters in support of Richards’ and Spradbery’s interpretations, and although no attempt was made to polarize these characters into derived and primitive states, van der Vecht (1977a:58) concluded that:

“(a) The Stenogastrinae are so different from the Polistinae and the Vespinae, both in morphological and ethological characters, that a taxon consisting of these three groups cannot be regarded as monophyletic.

(b) The Stenogastrinae are likely to have evolved from a solitary cell-building ancestor with elongate gastral petiole.

(c) Several characters . . . suggest that this ancestor was more closely related to the Zethinae than to the Eumenini.”

I (Carpenter, 1981) first treated the characters listed by van der Vecht in a phylogenetic context, polarizing them into primitive and derived states and showing that

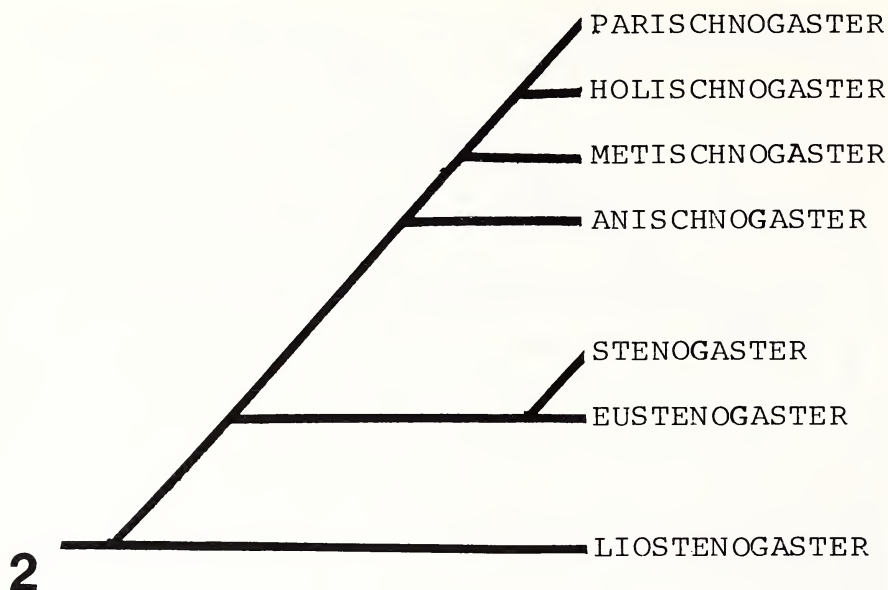


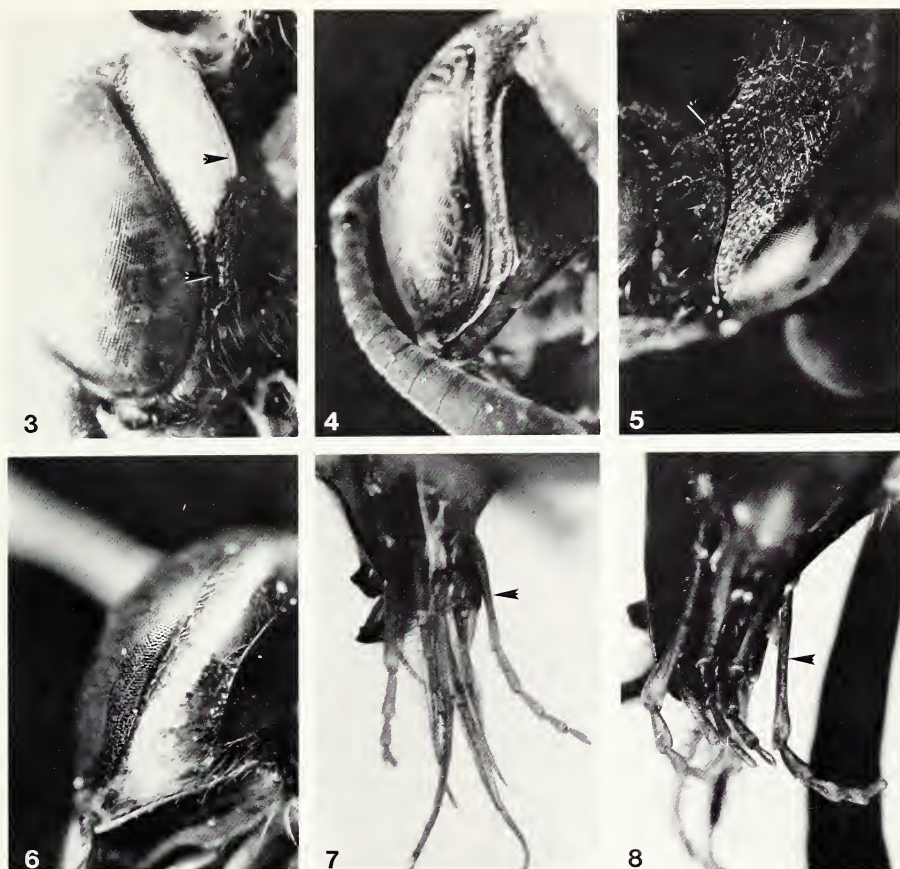
Fig. 2. Cladogram of stenogastrine genera.

his conclusions did not hold. Three other characters established the sister-group relationship between Stenogastrinae and Polistinae + Vespinae (Fig. 1). However, several recent authors (e.g., Hansell, 1982b, 1983; Pardi and Turillazzi, 1982; Turillazzi, 1986a), although citing Carpenter (1981), nevertheless continue to cite van der Vecht to the effect that stenogastrines are closely related to eumenines. It is thus necessary to recapitulate the conclusions of my previous paper. Following this I shall adduce further evidence to support the subfamily cladogram in Figure 1.

The characters listed for the Stenogastrinae by van der Vecht (1977a), and the polarities established by Carpenter (1981) are:

(1) Acroglossal buttons lacking. These are present in all other vespid subfamilies except Euparagiinae. Apomorphic loss in Stenogastrinae is the parsimonious interpretation considering other characters (Carpenter, 1981:18). Since it is an autapomorphy, this character is irrelevant to the question of the interrelationships of Eumeninae, Stenogastrinae, Polistinae and Vespinae.

(2) Occipital carina running towards hypostomal carina. Van der Vecht considered this similar to the state of some *Zethus*, where there is a forked carina, with an evanescent branch running towards the mandible as well as the hypostoma. As I pointed out previously (Carpenter, 1981:18), this similarity is superficial. In the groundplan state of Vespidae as a whole there are two carinae (Carpenter, 1981). The dorsal one, running from the vertex towards the hypostoma (Figs. 3–6, 9), is the occipital carina of other Hymenoptera. A second carina extends from the mandibular base dorsad along the posterior eye margin in Euparagiinae and some Masarinae (Fig. 3). Richards (1962) termed this the “ventral occipital keel,” but Snelling’s (1986) term “postocular carina” is more descriptive. The complete carina reaching the



Figs. 3-8. 3-6. Lateral view of head. 3. *Metapargia doddi* Meade-Waldo (Masarinae), 42 $\times$. The upper pointer indicates the occipital carina, the lower is on the postocular carina. 4. *Paramasaris brasiliensis* Giordani Soika (Masarinae), 50 $\times$. 5. *Zethus andinus* Brèthes (Eumeninae), 32 $\times$. Right side. The pointer indicates the branch running from the fused occipital and postocular carinae to the hypostomal carina. 6. *Liostenogaster nitidipennis*, 40 $\times$. 7-8. Palpi. The pointer indicates the second segment of the maxillary palpus. 7. *Anischnogaster iridipennis*, 50 $\times$. 8. *Eustenogaster* n. sp., 48 $\times$.

mandibular base seen in various solitary and social wasps is probably produced by confluence of these two carinae (Fig. 4), as suggested by Snelling for *Rolandia* (Masarinae), and this is the usual condition in Eumeninae. The forked carina (Fig. 5) found in most *Zethus* and closely related taxa does not occur in the genera usually considered relatively plesiomorphic in the "Zethinae," viz. *Discoelius*, *Protodiscoelius* and *Calligaster*. Therefore, the parsimonious interpretation is that a forked carina is probably apomorphic within Eumeninae, derived from a complete carina running to the mandibular base (Carpenter and Cumming, 1985:885 treated a forked carina as a groundplan state, but suggested that it could be considered as secondary). Under

either interpretation, the evanescent mandibular branch found in a few *Zethus* species is even further derived. Stenogastrinae possess none of these states, since they lack any trace of a postocular carina or forked composite carina (Figs. 6, 9). In fact, for their state to be synapomorphic with that found in species of *Zethus* with an evanescent mandibular branch, they would have to have originated as a subgroup of *Zethus* itself! No one has suggested this as a possibility, yet this is required for van der Vecht's interpretation to hold.

(3) Mandibles elongate and sometimes decussate, tridentate in females and "often more or less reduced" in males (Figs. 22–23). Pardi and Turillazzi (1982:19), following van der Vecht, stated that the mandibles of stenogastrines showed "concordance" with those of eumenines. Carpenter (1981:17) pointed out that decussate mandibles are plesiomorphic in Vespidae, and that all the subfamilies overlap in mandibular length. The tridentate condition is an autapomorphy. Both van der Vecht (1977a) and Carpenter (1981) noted that the mandibles are usually 4- or 5-toothed in Eumeninae (including "Zethinae"), Polistinae and Vespinae; this is also the case in Gayellini. The "reduced" male mandibles are not a groundplan character of the subfamily, but instead are apomorphic in particular genera (see below). This character therefore does not support van der Vecht's conclusions; it is uninformative on relationships.

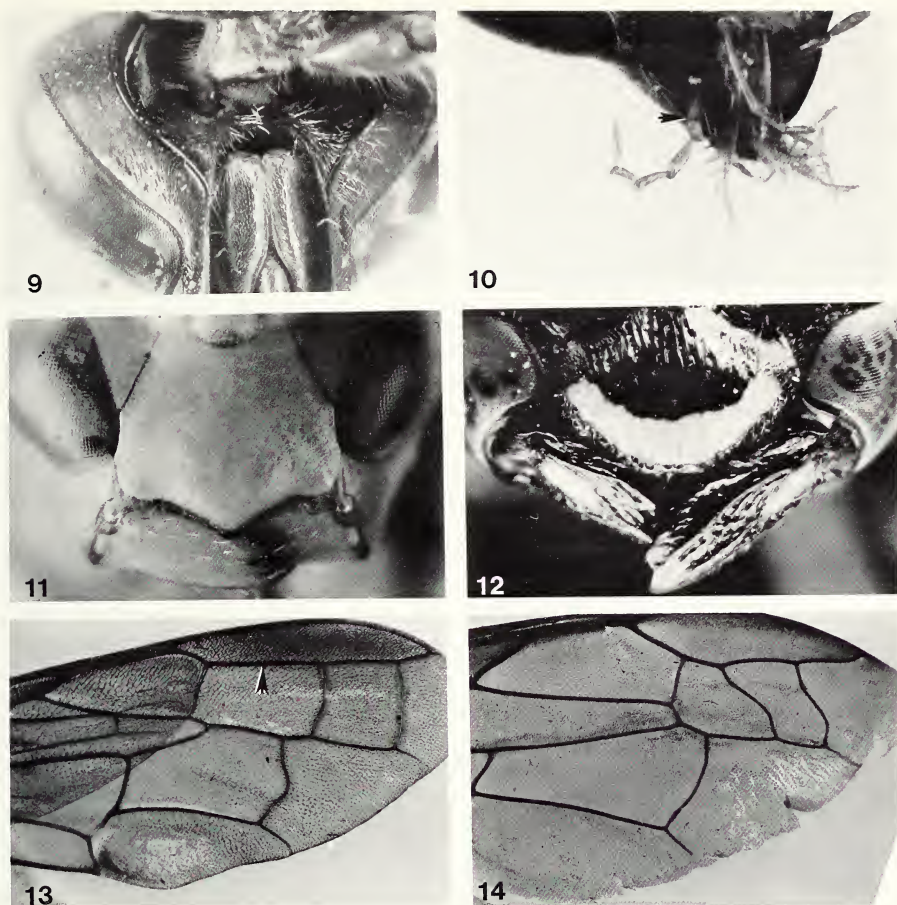
(4) Clypeus pointed apically in female, but lateral angles not projecting as in Polistinae (cf. Figs. 11 and 12). This is simply another autapomorphy (state 21c in Carpenter, 1981), and so uninformative. It is not similar to that of Eumeninae, contrary to Pardi and Turillazzi (1982). The clypeus is primitively truncate in the Eumeninae (Fig. 12; cf. Carpenter and Cumming, 1985), and is truncate or emarginate in nearly all species, being pointed only in a few derived taxa (e.g., *Rhynchalastor*).

(5) Antennal sockets far apart and separated from clypeus by long supraclypeal area (Figs. 21–22). I (Carpenter, 1981:19) did not deal with this state specifically, but stated "In the plesiomorph condition the anterior tentorial pits are close to the antennal sockets and the dorsal margin of the clypeus runs more or less straight between them." The state of a long supraclypeal area is unique to Stenogastrinae as a groundplan feature, and therefore is another autapomorphy, and so uninformative.

(6) Forewing marginal cell with RS almost straight (Fig. 13), hindwing with only two closed cells (Fig. 15). Only the second character was mentioned specifically by me (Carpenter, 1981), and I showed it is an autapomorphy of Stenogastrinae (only females were mentioned, but it is also true of males). The forewing character is also unique to Stenogastrinae, and so also an autapomorphy. Both characters are thus uninformative.

(7) Male genitalia, particularly the aedeagus and volsella, "are rather different from those of other dipterous wasps, but are perhaps most similar to those of Zethinae." I (Carpenter, 1981:22) discussed both the aedeagus and volsella more extensively, pointing out that both differed in detail in the two groups and that "Zethinae" were in fact more similar to Eumeninae. The condition in Stenogastrinae is autapomorphic.

(8) Pupal metasoma strongly bent at the articulation of segments I and II. Van der Vecht stated that this was also true of some *Zethus* species—but also some *Eumenes* s.l. Thus, it cannot show closer relationship of Stenogastrinae to "Zethinae" than to Eumenini (i.e., *Eumenes* s.l.), contrary to both van der Vecht (1977a) and Pardi and



Figs. 9–14. 9. *Eustenogaster luzonensis*, 28 $\times$. Ventral view of head. 10. *Parischnogaster depressigaster*, 44 $\times$. Palpi. The pointer indicates the second segment of the maxillary palpus. 11–12. Clypeus. 11. *Polistes xantholeucus* van der Vecht, 40 $\times$. 12. *Discoelius zonalis* (Panzer), 40 $\times$. 13–14. Forewing. 13. *E. eximia*, 15 $\times$. The pointer is in the second submarginal cell, and points to the RS vein. 14. *Dolichovespula maculata* (L.), 12.6 $\times$.

Turillazzi (1982). I (Carpenter, 1981:23) considered it convergent in species with long petioles.

None of these characters supports van der Vecht's conclusions; they are all uninformative on relationships. Most are autapomorphies, which, to be sure, do show that the Stenogastrinae is "so different" from Polistinae and Vespinae. But mere degree of difference indicates nothing about phylogenetic relationship (Hennig, 1966). These characters indicate only that the Stenogastrinae are truly monophyletic, which no one has questioned anyway. Carpenter (1981) cited three synapomorphies for

Stenogastrinae + (Polistinae + Vespinae): forewing marginal cell pointed onto costa (cf. Figs. 13 and 14), larval labrum not narrowed where it joins the clypeus and narrower than maximum width of clypeus, and the behavior of simultaneous progressive provisioning. All of these characters show some homoplasy (see Carpenter, 1981), but none of the characters cited by Richards, Spradbery or van der Vecht contradict this relationship—their characters simply say nothing about it. A related point is worth making. For van der Vecht's suggestion of closer relationship of Stenogastrinae to "Zethinae" than to Eumenini to be valid, not only would the three social wasp synapomorphies have to be convergent—but so would the autapomorphies of the Eumeninae as a whole. Carpenter (1981:26) cited four characters whose polarity could be clearly established which showed the monophyly of the Eumeninae as a whole. These are the parategula, hindcoxal carina, bifid claws and the shape of the larval labrum. For Stenogastrinae to be closely related to "Zethinae" they would have to be a subgroup of Eumeninae, and all of these features would either have to have been secondarily lost in Stenogastrinae or convergently gained at least twice in Eumeninae. There is no evidence whatsoever which compels the inference of such a massive degree of homoplasy, that is, no characters which actually suggest close relationship between hover wasps and a subgroup of potter wasps.

Before leaving this subject, I will point out additional behavioral characters which support the placement of the Stenogastrinae shown in Figure 1. As mentioned previously, all three social wasp subfamilies exhibit simultaneous progressive provisioning, that is a female tends several growing larvae. In all three groups, the female tends the larvae into the pupal stage, with females of Stenogastrinae removing the meconium after the pupal moult (Spradbery, 1975; Turillazzi, 1985b). Females of potter wasps which convergently show simultaneous progressive provisioning (species of *Synagris*, cf. Roubaud, 1911) do not show such extended care; they do not tend into the pupal stage. Second, Spradbery (1975) characterized the provisioning behavior in hover wasps as "intermediate" between the mass provisioning of potter wasps and the progressive provisioning of other social wasps. By this he meant that the amount of food provided in Stenogastrinae was sufficient to last a day or more. Mass provisioning is clearly primitive in Vespidae and progressive provisioning derived (Carpenter, 1981), thus stenogastrines may be considered more similar to higher social wasps, in showing a form of progressive provisioning, than potter wasps (mass provisioning). The form of this behavior in hover wasps may be the primitive condition. This character was interpreted by Pardi and Turillazzi (1982) as showing phylogenetic relationship between Stenogastrinae and Eumeninae, but as is obvious from the foregoing, this is a misinterpretation based on symplesiomorphy. Symplesiomorphy—the sharing of primitive features—is completely uninformative phylogenetically (Hennig, 1966). Third, all three social wasp subfamilies build complete nests, hanging free from the substrate except for the attachment point in the ground-plan condition (convergent in a few species of Eumeninae, Carpenter and Cumming, 1985; the astelocytarus condition found in some paper wasps is a further modification, since the primitive genera do not show this trait). The primitive condition in Vespidae is burrowing in the ground or using pre-existing cavities as a burrow. Another character in Spradbery's list can be interpreted as a fourth behavioral synapomorphy of the three social wasp subfamilies. This is whether two or more females

are present on a newly founded nest, characterized by Spradbery as not occurring in Eumeninae (it actually does occur in a few species; cf. West-Eberhard, 1978), "frequent" in Stenogastrinae, "common" in Polistinae and "rare" in Vespinae. In the evolutionary model for the origin of social behavior of West-Eberhard (1978), the condition of nest-sharing corresponds to the primitively social stage. Polistinae + Vespinae, being all eusocial, are inferred to have a common ancestor which evolved through a stage of casteless nest-sharing. Therefore, if the ground-plan condition in Stenogastrinae is nest-sharing, this would be another synapomorphy of these three groups. Stenogastrinae are still frequently characterized as having solitary species (e.g., Hansell, 1982a; Pardi and Turillazzi, 1982; Ohgushi et al., 1983a), although as noted above they are actually at least subsocial (Iwata, 1967, 1976). But many species do not consistently exhibit nest-sharing. For example, in *Stenogaster concinna* (Spradbery, 1975), *Eustenogaster calyptodoma* (Hansell, 1987), *Parischnogaster mellyi* (Hansell, 1982a, 1983), *Holischnogaster gracilipes* (Hansell, 1986a), and *Liostenogaster flavolineata* (Hansell et al., 1982) colonies with only a single female are common. But in all of these species, multiple-adult nests also occur. Thus, on present evidence, nest-sharing appears to be universal in the subfamily, but it does not characterize the entire colony cycle (as is also the case in many Polistinae and Vespinae). The single female nests found in these species may have been recently founded, since a single foundress appears to be the general mode of colony foundation (cf. references above, and Krombein, 1976; Yamane et al., 1983a, b; Turillazzi, 1982, 1985a). Other adults are then added either by emergence of daughters which remain on the natal nest for a period (e.g., Spradbery, 1975; Krombein, 1976; Hansell, 1983, 1986a, 1987; Turillazzi, 1985a) and/or joining behavior (e.g., Yoshikawa et al., 1969 but cf. Hansell, 1982b; Hansell et al., 1982; Turillazzi, 1985a, c). At the very least, facultative nest-sharing is then most parsimoniously inferred to be the ground-plan state of Stenogastrinae as a whole. As such it is a synapomorphy of all the social wasps, for assuming West-Eberhard's model (cf. Carpenter, 1988) it is then most parsimoniously inferred to be the ground-plan state of their common ancestor. Other behavioral similarities are probably synapomorphies of Stenogastrinae + Polistinae + Vespinae as well (see below).

These interpretations of behavioral data are contrary to those of authors such as Pardi and Turillazzi (1982) and Turillazzi (1985a, b, 1986a), who argue that the similarities in social behavior among Stenogastrinae and Polistinae + Vespinae are convergent. But this view only followed from van der Vecht's scheme of phylogenetic relationships, which these authors adopted. As discussed above and in Carpenter (1981), that scheme is untenable. The available evidence best supports the cladogram of Figure 1, and so the development of social behavior in stenogastrines is not independent of that in the other social wasp subfamilies. Evolution subsequent to the diversification of their common ancestor has produced differences in various details of the social behavior of these three groups, but where behavioral similarities occur in the groundplans of the subfamilies, such similarities must be inferred to be the product of common ancestry (Hennig, 1966; Farris, 1983). As Carpenter (1981: 30) stated: "Exclusion of the stenogastrines from discussion of social behaviour in the Vespinae + Polistinae may lead to the loss of valuable evolutionary perspective." The reverse is equally true.

GENERIC RELATIONSHIPS

Materials and Methods

The characters studied were drawn from those used by previous authors of taxonomic or behavioral papers on these wasps. Autapomorphies of the subfamily already discussed by Carpenter (1981) were not included. The 24 adult morphological characters discussed below were examined on pinned specimens; all are deposited in the Museum of Comparative Zoology, U.S. National Museum, or Australian National Insect Collection. The species examined are listed in the appendix. Male genitalia were dissected, slightly cleared in lactophenol, and examined in glycerin. Illustrations were made with a Wild M-400 photomicroscope and Kodak T-Max 400 film. Morphological terminology is as in Carpenter (1981) and Carpenter and Cumming (1985). Larvae of *Liostenogaster flavolineata*, *Eustenogaster calyptodoma*, *Holischnogaster gracilipes* and *Parischnogaster striatula* were provided by Dr. M. H. Hansell. Larvae of *E. eximia*, *E. hauxwellii*, *E. micans*, *P. mellyi* and *P. spp.* in the collection of the British Museum were also studied. Data on other species were drawn from the literature as noted. Behavioral data were also drawn from the literature.

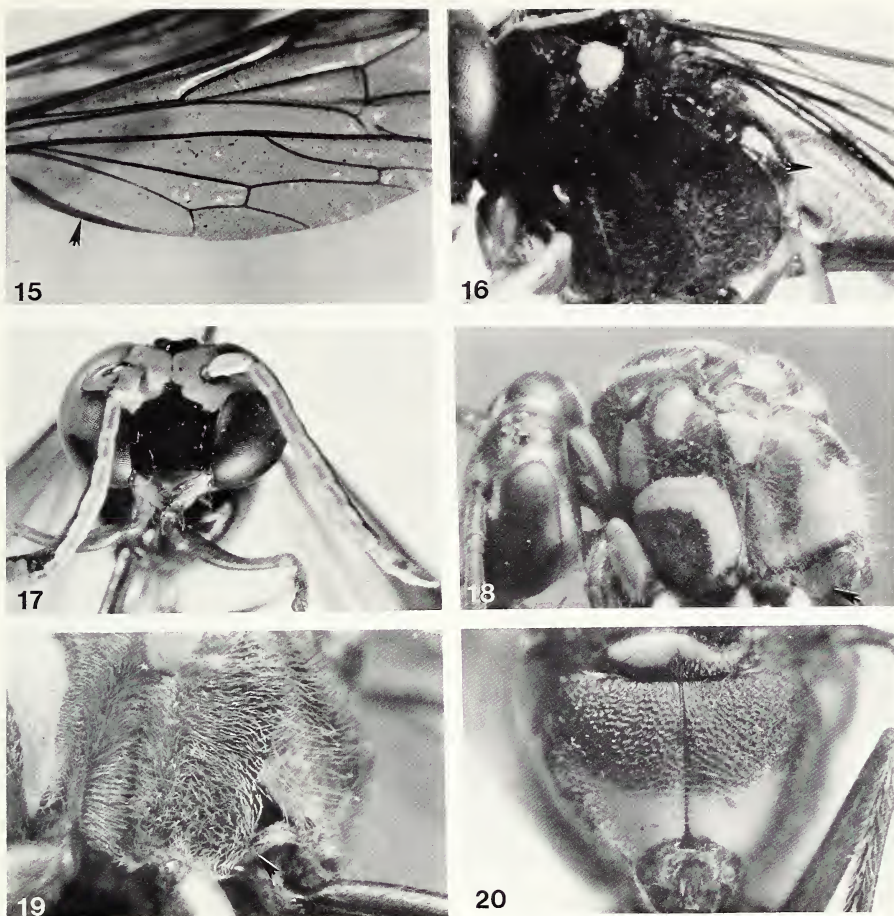
Character polarities were established by considering all other vespid subfamilies as outgroups. The ten morphological characters which varied among the genera (that is, were informative concerning relationships) were coded as in Tables 1 and 2, and subjected to quantitative cladistic analysis. This was performed using the PHYSYS® system by J. S. Farris and M. F. Mickevich, State University of New York at Stony Brook and Maryland Center for Systematic Entomology, as implemented on the VAX 11/780 computer running VMS at Harvard University. The behavioral characters were analyzed separately because of the ambiguity of many of these features. As shown below, at the generic level they are congruent with the morphological results.

CHARACTERS

The Wings

1. Forewing second submarginal cell (IRS). In other Vespidae (Fig. 14) the anterior border of the second submarginal cell (formed by the RS vein) is much shorter than the posterior border (formed by the M vein). Only in Stenogastrinae are the anterior and posterior borders of approximately equal length, giving a rectangular appearance to the cell (Fig. 13). This unique feature is found in all Stenogastrinae, and so is an autapomorphy of the subfamily.

2. Hindwing. In males of the genus *Eustenogaster* (Fig. 15) there is a pigmented area along the posterobasal edge of the hindwing proximal to the preaxillary excision (edge of the clavus of Wootton, 1979). This character was mentioned in the diagnosis of this genus by van der Vecht (Yoshikawa et al., 1969:165). It is unique to *Eustenogaster*, and so is an autapomorphy, showing the monophyly of the genus. *Eustenogaster* males also lack the short fringe of hairs found along the posterior edge of the wing in other vespids. This fringe of hairs becomes greatly elongated in *Metischnogaster* (Fig. 16), and is an autapomorphy of that genus. In female *Metischnogaster* the hairs are moderately longer than in other hover wasps, but in males they are longer than the distance between vein 1A and the posterior margin of the wing.



Figs. 15–20. 15. *Eustenogaster fulvipennis*, 22 $\times$. Hindwing. The pointer indicates the posterobasal pigmented area. 16. *Metischnogaster cilipennis* (Smith), 32 $\times$. Lateral view of metasoma. The pointer indicates the elongate fringe of hairs on the hindwing. 17. *M. cilipennis* male, 20 $\times$. 18–19. The pointer indicates the propodeal valvula. 18. *Liostenogaster nitidipennis*, 19 $\times$. Lateral view of metasoma. 19. *Parischnogaster depressigaster*, 40 $\times$. Lateral view of propodeum. 20. *Anischnogaster spilaspis*, 34 $\times$. Posterior view of propodeum.

Head

3. Occipital carina. In *Liostenogaster* the occipital carina runs towards the hypostomal carina but evanesces before reaching it (Fig. 6). There is no trace of the postocular carina, which is derived. In all other stenogastrine genera the occipital carina reaches the hypostomal carina and fuses with it (Fig. 9). This is a further derived condition, and so this state is a synapomorphy grouping all the genera apart from *Liostenogaster*.

4. Male clypeus. As mentioned above, in female Stenogastrinae the clypeus is

pointed apically. This is also true of males in most of the genera (Figs. 17, 21), although the pointing is not generally as pronounced as in females. In *Stenogaster* the male clypeus is rounded apically, so that it appears broadly rounded (Fig. 22). The clypeus is also depressed apically. This state is clearly apomorphic, but is approached in *Eustenogaster*. In that genus (Figs. 23 is the least developed condition) the males have the clypeus apically rounded into a blunt angle, but the condition is not as different from the female, and the clypeus is not depressed apically. Males of a few other species have the clypeus slightly rounded apically (*Parischnogaster depressigaster*, *Anischnogaster dubia*), but other species in these particular genera have a pointed clypeus. An apically rounded clypeus in the male may therefore be treated as a synapomorphy between *Stenogaster* and *Eustenogaster*, with the ventral depression being an autapomorphy of *Stenogaster*.

5. Male mandibular teeth. As noted above, tridentate mandibles are an autapomorphy of the subfamily. Reduction from this number in males of some of the genera is then further apomorphic. This occurs in *Metischnogaster*, where the mandibles are bidentate. It also occurs in an undescribed species of *Liostenogaster*. In *Anischnogaster* the proximal teeth are quite blunt, appearing almost fused in some species (*A. iridipennis* and *loriai*; cf. figs. in van der Vecht, 1972). But the most notable reduction occurs in *Stenogaster* and *Eustenogaster*, where both of the proximal teeth are lost (Figs. 22, 23). Traces of a proximal tooth remain in *Eustenogaster*, in the form of a blunt inner angle (Schulthess, 1914: fig. B), but in *Stenogaster* even this is lost and the mandible is narrowed and curved apically (Fig. 22). Reduction to one tooth is thus a synapomorphy of *Eustenogaster* + *Stenogaster*, with distal narrowing and curving an autapomorphy of the latter genus. The bidentate mandibles of *Metischnogaster* are an autapomorphy of that genus, but the relationship between this state and the unidentate condition is unclear. Although it seems straightforward to treat the states as part of a linear transformation series, as in Table 1, the results of analysis with other characters (Fig. 2) require homoplasy under this interpretation. The transformation in *Metischnogaster* occurs independently of that in the common ancestor of *Eustenogaster* + *Stenogaster*. It would be more parsimonious to treat both the bidentate and unidentate conditions as arising independently from the tridentate state. The initial coding of this character (Table 1), however, does not affect the results other than to introduce some homoplasy, so it is retained here.

6. Labial palpi. In the Stenogastrinae, the first segment of the labial palpus is greater than or approximately equal to the combined length of segments 2-4 (Fig. 8; figs. in van der Vecht, 1975, 1977a). The general condition in Vespidae as a whole is to have the two basal segments of approximately equal length. Therefore, the condition in hover wasps is derived, and so is another autapomorphy of the subfamily. As stated by Schulthess (1914:254), the first segment is relatively longer in *Eustenogaster* + *Stenogaster* than in the rest of the subfamily.

7. Maxillary palpi. In Vespidae as a whole the segments of the maxillary palpus are all of approximately equal length. This is the groundplan condition, but in hover wasps segment 2 is frequently elongate. In *Liostenogaster*, *Holischnogaster* and *Anischnogaster* it ranges in length from 1.5 to about twice the length of segment 3 (Fig. 7; van der Vecht's 1977a key is misleading in regard to latter genus, but his 1972 revision characterizes the feature correctly). In *Stenogaster* and *Eustenogaster* (Fig. 8) it is three times or more the length of segment 3 and about equal to or greater



Figs. 21-26. 21-23. Clypeus of male. 21. *Holischnogaster gracilipes*, 48 $\times$. 22. *Stenogaster concinna*, 32 $\times$. 23. *Eustenogaster hauxwellii*, 34 $\times$. 24-26. Antennae. 24. *Parischnogaster depressigaster* female, 25 $\times$. 25. *H. gracilipes* male, 20 $\times$. 26. *S. concinna* male, 16 $\times$.

than the combined length of segments 3-6. However, in *Parischnogaster* and *Metischnogaster* (Fig. 10) segments 2 and 3 are of approximately equal length. Therefore, if elongation of segment 2 is an apomorphic groundplan feature of Stenogastrinae, it has undergone some reversal. It may be better to regard the elongation as an apomorphic tendency arising several times, since the differences between most of the genera are not very great. However, this is not true of the greater elongation of segment 2 in *Eustenogaster* + *Stenogaster*; this is clearly a distinguishing feature, as realized by Schulthess (1914:254). It is another synapomorphy of these two genera.

8. Antennae. Several modifications of the antennae are found in hover wasps. The antennae are usually somewhat swollen apically, but flagellomere 8 (females) or 9 (males) is usually less than twice the width of flagellomere 2. However, in *Holischnogaster* and *Parischnogaster* (Figs. 24, 25) the swelling is more extreme, so that flag-

Table 1. Informative characters and their inferred polarities as coded in alphanumeric format for the CREAD input command of PHYSYS. The plesiomorphic state is leftmost. States separated by commas are considered to have evolved separately from the plesiomorphic state.

3. Occipital carina:	GAP-FUSED
4. Male clypeus:	POINT-ROUND
5. Male mandibular teeth:	THREE-TWO-ONE
7. Maxillary palpi:	EQUAL-GREATER
8. Antennae:	NORMAL-CLUB,FLAT,TIPPED
14. Propodeal valvula:	ROUND-NARROW
16. Propodeal sculpture:	STRIATE-SMOOTH,PUNCTATE
20. Segment II:	NORMAL-PETIOLE
22. Parameral spine:	SPINOSE-FLAT
24. Aedeagus:	NORMAL-DILATED

ellomere 8 or 9 is much more than twice the width of the second flagellomere. This is a synapomorphy of these two genera, but the state is approached in a few other species (e.g., *Anischnogaster spilaspis*), somewhat weakening it. Other modifications are autapomorphies of two other genera. In *Metischnogaster* (Fig. 17) the flagellomeres are noticeably flattened ventrally in the male, and in *Stenogaster* (Fig. 26) the apical flagellomere of the male is truncate and flattened, as well as often dilated (figures in van der Vecht, 1975).

9. Vertex. As noted by van der Vecht (1977a) in his description of the genus, *Metischnogaster* has an impressed median longitudinal groove on the vertex between the ocelli and occipital carina. Although a faint impression sometimes appears in other hover wasps, none have a clear line, and so this feature is an autapomorphy of *Metischnogaster*.

Mesosoma

10. Pronotum. Hover wasps lack the dorsal pronotal carina and pretegular carina which are found in the groundplans of all other vespidae subfamilies. These losses are autapomorphic, further confirming the monophyly of the Stenogastrinae.

11. Notauli. In *Metischnogaster* there are distinct, deeply impressed notauli on the scutum (van der Vecht, 1977a, termed them prescutal furrows). Although this seems similar to the primitive hymenopterous condition, other stenogastrines lack notauli—shallow traces occur only in some species of *Parischnogaster* (*P. depressigaster* and *nigricans*) and *Anischnogaster*. Therefore, the deeply impressed condition in *Metischnogaster* is probably apomorphic, not primitive. As such this character is an autapomorphy of the genus.

12. Male metapleuron. Van der Vecht (1977a) called attention to the fact that in males of *Metischnogaster* the metapleuron and part of the mesepisternum and propodeum are sunken and densely pubescent, and this area is bordered posteriorly by a strong carina (Fig. 16). This is an outstanding autapomorphy of the genus. Some species of *Parischnogaster* have dense pubescence on this part of the mesosoma (Fig. 19), but this is not similar.

13. Scutellum. Van der Vecht in the diagnosis of *Eustenogaster* (Yoshikawa et al.,

1969) used the character of the scutellum with a sharp, median longitudinal carina as a distinguishing feature. This is an autapomorphy of the genus. Other stenogastrines have at most faint traces of such a carina anteriorly.

14. Propodeal valvula. The relatively large propodeal valvula of *Eustenogaster* was noted by Carpenter (1981:20). A similar, albeit smaller, valvula is found in *Liostenogaster*, *Stenogaster* and *Anischnogaster* (Fig. 18). It is also narrower in the latter two genera. No submarginal carina is present in stenogastrines, but the valvula is well differentiated from the propodeum, appearing similar to the groundplan condition in Eumeninae and other social wasps. In *Metischnogaster*, *Holischnogaster* and *Parischnogaster* the valvula is much narrower (Fig. 19). In *Metischnogaster* it is essentially completely reduced; in *Holischnogaster* and *Parischnogaster* it is completely attenuate only posteriorly, and narrow but present anteriorly. The state of a posteriorly reduced valvula is thus a synapomorphy of these three genera, with further reduction autapomorphic in *Metischnogaster*.

15. Propodeal orifice. One of the distinguishing features of *Stenogaster* is a raised lamella on the propodeum just dorsal to the propodeal orifice (Fig. 27). This is not similar to the condition in other Vespidae where there may be a submarginal carina or a continuation of the propodeal valvula above the orifice; the lamella in *Stenogaster* is completely separated from the propodeal valvula. The state in *Stenogaster* is unique, and so an autapomorphy of the genus.

16. Propodeal sculpture. There are various forms of sculpturing on the propodeum in Vespidae. Most species have the propodeum punctate, and the punctation may be quite coarse. Transverse ridges on the posterior face of the propodeum are also quite common, as in *Polistes*. There are three states in the Stenogastrinae. In *Stenogaster*, *Metischnogaster*, *Holischnogaster* and some species of *Parischnogaster* (e.g., *P. depressigaster* and *timida*) there are transverse ridges on the posterior face of the propodeum (Figs. 27, 28). The ridges may be quite weak, as in *Stenogaster* (Fig. 27). In *Anischnogaster* and other species of *Parischnogaster* (Fig. 20) there are no ridges, but the punctation is well developed, and irregular transverse rugae may somewhat resemble the ridges found in other stenogastrines. In *Liostenogaster* and *Eustenogaster* (Fig. 18) the propodeum is smooth and shining, lacking both ridges and punctation (although pubescent). This last state is clearly derived, as it is relatively uncommon in Vespidae and does not characterize the groundplan of any of the other subfamilies. But the transformation series of the character as a whole is unclear. Either a striate or punctate propodeum is plesiomorphic in the subfamily, but it is not obvious which, especially considering that *Parischnogaster* is variable in this regard. The outgroups are variable as well, although the punctate condition is the more general. Any interpretation requires homoplasy, but considering that the striate condition occurs in "groups otherwise having little in common" (Kluge and Farris, 1969; cf. Farris, 1982), that is, several genera separated on the cladogram (Fig. 2), it is treated here as the plesiomorphic condition. The punctate condition in *Anischnogaster* is then an autapomorphy, convergent in some *Parischnogaster* (note that under any interpretation, given the cladogram of Figure 2, the striate condition must be treated as the groundplan state of the latter genus). A smooth propodeum is also convergent; as shown by Figure 2 other characters indicate that *Liostenogaster* and *Eustenogaster* are not closely related.

17. Male foreleg. Pagden (1958: fig. 21b) showed the row of peculiar spatulate setae

on the underside of the foretibia in males of *Metischnogaster*, first noted by Smith (1857). Pagden also figured (1958: figs. 21c, d) the ventral production of some of the fore tarsomeres into spines in males of this genus. Both states are autapomorphies of *Metischnogaster*, being unique.

18. Male midleg. Van der Vecht (1977a) used the condition of asymmetrical mid-tarsi of males in *Parischnogaster* as a key character in distinguishing the genus. It is autapomorphic, unique in the subfamily. Absence of this condition was a major reason for van der Vecht's distinction (1977a:73) of *Holischnogaster* as a separate genus, for, as he stated, it is closely related to *Parischnogaster*.

Metasoma

19. TII spiracles. In *Metischnogaster* (Fig. 31) the spiracles of metasomal segment II are visible in dorsal view, whereas they are only visible laterally in other hover wasps. This is an autapomorphy of *Metischnogaster*; it is unique.

20. Segment II petiole. In *Anischnogaster*, *Metischnogaster*, *Holischnogaster* and *Parischnogaster*, metasomal segment II is distinctly petiolate basally (Figs. 31, 32). A similar state occurs in various Eumeninae (e.g., *Paramischocyttarus*) and Polistinae (*Belonogaster*), but is not ancestral for either subfamily. Thus a petiolate segment II is derived in Stenogastrinae. In *Liostenogaster*, *Eustenogaster*, and *Stenogaster* segment II is not petiolate, but merely narrowed basally (Fig. 30). This is the primitive condition for the subfamily, and so a petiolate segment II is a synapomorphy for *Anischnogaster* + (*Metischnogaster* + (*Holischnogaster* + *Parischnogaster*)).

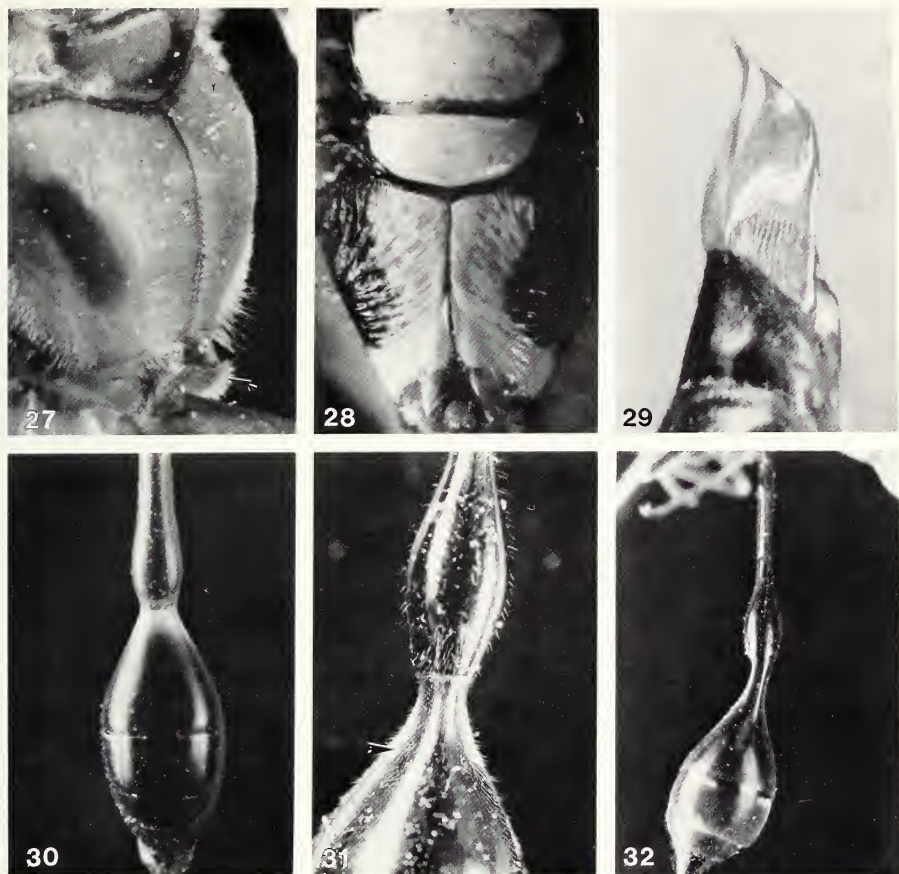
21. Male SVII. In male Stenogastrinae, the sternum of metasomal segment VII is noticeably flattened, whereas the usual condition in Vespidae is to have it rounded as in females. The state in Stenogastrinae is thus another autapomorphy of the subfamily.

Male Genitalia

Certain stenogastrine autapomorphies in the male genitalia were discussed by Carpenter (1981:22, 27). These were the volsella with the digitus curved apically and desclerotized proximally, and the aedeagus very attenuate apically with the ventral processes small and narrow.

22. Parameral spine. In *Holischnogaster* and *Parischnogaster* the parameral spine is greatly dilated basally (Figs. 29, 33), so that its height is nearly equal to that of the paramere in lateral view. This character was noted by Schulthess (1914: figs. G and H), and was used as a key characteristic by van der Vecht (1977a). Charnley (1973:55–56) misinterpreted the dilated spine as a subdivision of the paramere. The state is unique in the Vespidae, which typically have the spine elongate (Fig. 34), and so is an outstanding synapomorphy of *Holischnogaster* + *Parischnogaster*.

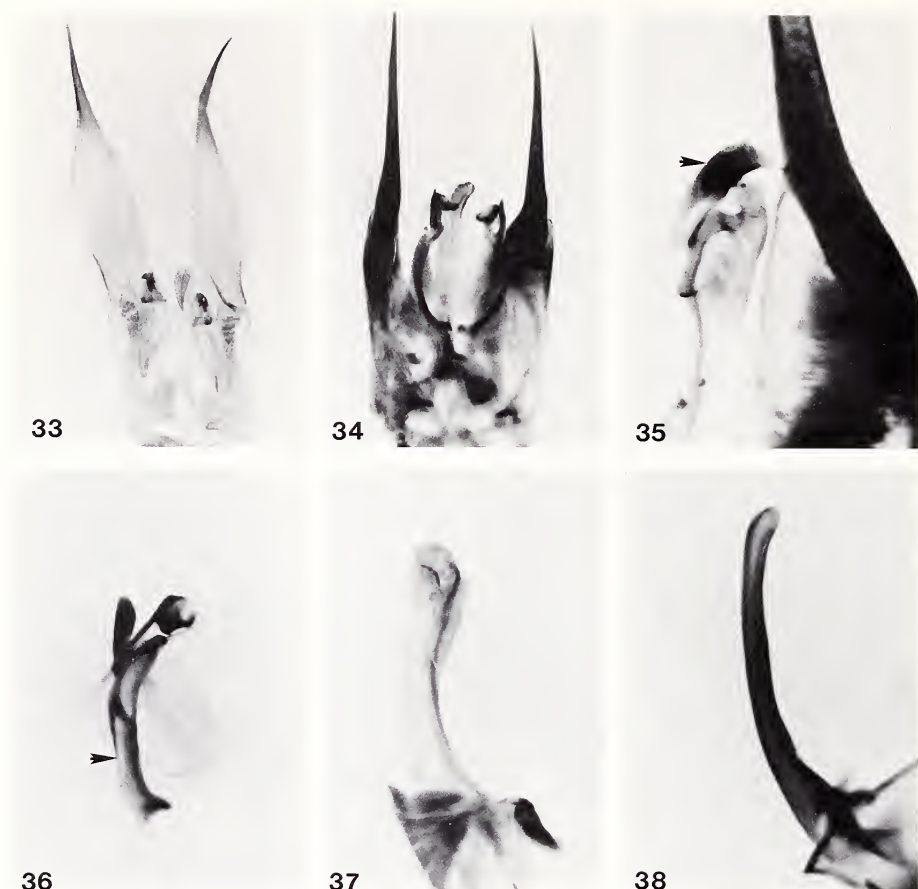
23. Volsella. The cuspis and lamina volsellaris appear completely fused in Stenogastrinae (Figs. 35, 36). This is a derived condition in Vespidae, which has arisen in several subfamilies (Carpenter, 1981). The cuspis is more or less rounded apically and the digitus scimitarlike and completely reduced proximally (Fig. 35; it remains a separate structure, contrary to what is depicted in van der Vecht, 1977a: fig. 26). The form of the volsella differs mostly in minor detail among the genera, except in



Figs. 27–32. 27–28. Propodeum. 27. *Stenogaster concinna*, 46 $\times$. Lateral view. The pointer indicates the lamella dorsal to the propodeal orifice. 28. *Metischnogaster drewseni*, 60 $\times$. Posterior view. 29. *Parischnogaster nigricans* male, 50 $\times$. Parameral spines. 30–32. Metasoma. 30. *S. concinna*, 14 $\times$. 31. *M. drewseni*, 32 $\times$. The pointer indicates the spiracle on Tergum II. 32. *P. mellyi*, 14 $\times$.

Stenogaster. In this genus, the cuspis + lamina is strongly narrowed medially (Fig. 36). This is a unique derived condition, another autapomorphy of *Stenogaster*.

24. Aedeagus. In *Metischnogaster* the aedeagus has a pair of small projections located laterally and subapically. In *M. cilipennis* they are blunt (van der Vecht, 1977a: fig. 27) but in *M. drewseni* they are sharp and toothlike (van der Vecht, 1977a: fig. 37). Such projections are not found elsewhere in the Stenogastrinae, and so their presence is another autapomorphy of *Metischnogaster*. Another feature of the aedeagus may be a synapomorphy of *Metischnogaster* + (*Holischnogaster* + *Parischnogaster*). In these genera, the aedeagus is apically strongly compressed, and the apex is dilated in lateral view (Fig. 37; van der Vecht, 1977a: figs. 27, 37, 47). The dilation



Figs. 33–38. Male genitalia. 33–34. Ventral view. *Holischnogaster gracilipes*, 40 $\times$. 34. *Stenogaster adusta*, 38 $\times$. 35–36. Lateral view of volsella. 35. *Eustenogaster eximia*, 64 $\times$. Right side. The pointer indicates the digitus. 36. *S. adusta*, 64 $\times$. Left side. The pointer indicates the lamina volsellaris. 37–38. Lateral view of aedeagus. 37. *Metischnogaster cilipennis*, 64 $\times$. 38. *S. concinna*, 64 $\times$.

is least pronounced in *Parischnogaster mellyi* among the species I have examined, where the apex is just slightly thickened. The generality of this character should be checked further in other species of *Parischnogaster*, but the condition does not occur in other hover wasps (Fig. 38), and so is treated here as a synapomorphy of the three genera showing it.

Larvae

Use of the larvae as a source of taxonomic characters continues to be hampered by the paucity of descriptions. Thanks to M. H. Hansell, I have been able to examine specimens of one genus for which the larvae are undescribed (*Holischnogaster*), but

no material or description of species of *Metischnogaster* or *Anischnogaster* have been available. I have therefore not attempted to make a very exhaustive study of the larvae, but only provide here some general descriptive notes.

The general form of the larva is basically as in other Vespidae: fusiform, unpigmented except for the head capsule and mandibles, ecdysial line and parietal bands present, galeae and palpi conical and somewhat projecting, spinneret a transverse slit without raised lips, 10 circular spiracles present, spiracular atria unarmed, pleural lobes present, anus a straight terminal slit. The first spiracle is about twice the diameter of the succeeding spiracles, as occurs in some Polistinae. Abdominal segments 1–6 have prominent dorsal lobes. The presence of long setae on the prothorax is an autapomorphy of the subfamily (Carpenter, 1981). Characters of the head and mouthparts are further discussed below.

It should be noted here that several recent authors have stated that a distinguishing feature of Stenogastrinae is a reduced number of larval instars. The condition in other Vespidae which have been studied is five, e.g., Vespinae (Spradbery, 1973) and the eumenine *Ancistrocerus antilope* (Cooper, 1966). Five instars have also been reported in Stenogastrinae (Iwata, 1967). However, Hansell (1982a, 1986a) and Turillazzi (1985b) have suggested that there are only three or four instars, which if true would be an autapomorphy, but neither author established this. They simply cited frequency distributions of head capsule widths, with Hansell (1982a) citing "Dyar's rule" on the geometrical size progression of head widths of instars—although he also cited Richards (1949) to the effect that the rule does not hold in general. Both Hansell and Turillazzi disputed Iwata's partitioning of his own data into five instars only by arguing that the measurements fit as well or better into fewer size classes. But as pointed out by Cooper (1966), for definitive demonstration of the number of larval instars three conditions must be satisfied:

- "(1) the first instar larva must be identified with certainty, generally by witnessing hatching, (2) exuvia must be removed when shed, or very shortly thereafter, and (3) closely and appropriately spaced observations must be continued from hatching to the emergence of the imago."

None of these conditions were met in Hansell's or Turillazzi's cited papers. It is possible that the earliest instars were lumped together; as shown by Buysson (1903) and Cooper (1966) the first instar may not even shed the chorion until the first moult in Vespidae. Although the hatching sequence and immediate shedding of the chorion has been observed in *P. mellyi* by Turillazzi (1985d), study of other species is required to establish the generality of this in Stenogastrinae. And collection of exuvia is required to ascertain the number of larval instars with complete certainty. At present there is no clear case for accepting that a reduced number occurs.

25. Head. A labrum narrower than the maximum width of the clypeus and not narrowed where it joins the clypeus is a synapomorphy uniting the three social wasp subfamilies (Carpenter, 1981), although some polistines show reversal of this feature. All the stenogastrine species with undescribed larvae which I have examined also show this character, the labrum being just over half the width of the clypeus. The ventral margin of the labrum is truncate to slightly bisinuate but not bilobed as it is in Vespinae. The clypeus is much wider than high, as is usually the case in Vespidae, and the frontoclypeal suture is well developed. The anterior margin of the clypeus

is well below the level of the mandibular bases. *Liostenogaster flavolineata* differs from the other stenogastrine species examined in having the entire head capsule pigmented, whereas the pigmentation is confined to the lower part of the head capsule in the other species. It is unclear whether any significance should be attached to this.

The most notable feature by which larval Stenogastrinae differ from other Vespidae is in the presence of an antennal papilla. This is an elongate projection in all species examined; other vespids have sensilla on the antennal plate. Other Aculeata show considerable variation in the presence of papillae or sensilla on the antennal plate (Evans, 1987), and so a papilla may not be homologous as a primitive feature among aculeate families. But even if it is, the presence of one in Stenogastrinae is then an apomorphic reversal, since the subfamily is relatively derived in the Vespidae (Fig. 1; Carpenter, 1981).

26. Mouthparts. Iwata (1967) stated that the mandible of the stenogastrines he examined was bidentate, and his figs. 6 and 9 for *Liostenogaster nitidipennis* and *Parischnogaster mellyi* appear to show this, but it is incorrect. As Richards (1978: 14) stated, the larval mandibles are tridentate in stenogastrines, with one of the teeth smaller and set back on the dorsal margin (as figured for *Stenogaster concinna* by Spradbery, 1975; fig. 10). Tridentate mandibles are general in the species I have examined, including *P. mellyi*; this is plesiomorphic in the Vespidae (Carpenter, 1981). However, the arrangement of the teeth does not seem to occur in the same form in other vespids (cf. Evans, 1987, for summary), and so this may actually be derived.

Behavior

Use of behavioral characters is somewhat hampered by lack of sufficient detail in published reports, but thanks to the efforts of Hansell, Turillazzi, Ohgushi, and other workers something is now known for all of the genera. Although necessarily tentative, because of the relatively few published accounts, some inferences concerning the evolution of behavioral traits may be drawn. Most of the characters discussed here are placed in a cladistic context for the first time. The emphasis is on reconstruction of groundplan conditions consistent with parsimony, based on optimization (Farris, 1970) of behavioral characters on the cladograms (Figs. 1 and 2). Certain characters which show relationship to other subfamilies are also treated above.

27. Nest material. The use of soil in the construction of nests is clearly more primitive than the use of material of plant origin in the solitary vespids, where only a few species use the latter in a derived type of nest (cf. Carpenter and Cumming, 1985). But this is probably not the case in the social wasps. Polistinae + Vespinae employ plant material; only a few species of *Polybia* use mud (Richards, 1978). The situation is unclear in Stenogastrinae, because both materials are employed in several genera. Soil is used in the one species of *Stenogaster* reported (*S. concinna*, Spradbery, 1975), at least three species of *Liostenogaster* (*L. varipicta*, Williams, 1919; *L. flavolineata*, Pagden, 1958; *L. nitidipennis*, Iwata, 1967; unidentified species, Pagden, 1958; Iwata, 1967; Yoshikawa et al., 1969; Ohgushi et al., 1983b, c, 1985, 1986), and one species of *Anischnogaster* (*A. iridipennis*, van der Vecht, 1972). Plant material alone is employed in the other genera (summary in Iwata, 1976; *Holischnogaster* reported by Hansell, 1986b), as well as species of *Liostenogaster* (unidentified species, Pagden, 1958, Ohgushi et al., 1983b, c) and one species of *Anischnogaster* (*A. laticeps*,

van der Vecht, 1972). Some species have been reported to include both in the same nest (Pagden, 1958; Ohgushi et al., 1983b, c) or to use one or the other type of material (*Parischnogaster mellyi*, Ohgushi et al., 1983b, c). Given this variation, the polarity of this character within the subfamily is difficult to assess, and under any interpretation there is considerable convergent evolution. Because the sister-group of this subfamily uses plant material, one might be inclined to treat this as the groundplan condition in hover wasps as well, and hence another synapomorphy of the social wasps. However, Hansell (1985) has shown considerable differences between the paper made in Stenogastrinae and Polistinae + Vespinae, so the hover wasps are perhaps primitive relative to other social wasps even if use of paper is a synapomorphy of the three subfamilies.

28. Nest architecture. As noted above, the construction of nests entirely from gathered material and which project freely from the substrate is a synapomorphy of the social wasps. Stenogastrinae differ from the other two social subfamilies in not beginning the nest with a petiolate cell (Yoshikawa et al., 1969; van der Vecht, 1977b); this must be primitive. Few generalizations can be made beyond this, for within the subfamily there is extreme diversity in nest architecture and substrate selection. This has been documented by Williams (1919), Pagden (1958), Iwata (1967), Yoshikawa et al. (1969), Ohgushi et al. (1983b, c, 1985, 1986) and Ohgushi and Salmah (1986). Although specific differences in nest architecture may be relatively constant and have been used in the recognition of new taxa (Sakagami in Yoshikawa et al., 1969; Sakagami and Yoshikawa, 1968), the architecture may be radically different within species, depending on attachment (Iwata, 1967; Hansell, 1981). Iwata (1967, 1976) divided the myriad shapes into two basic types, those with combs of cells and those where the cells are arranged in vertical series. Features common to the two types included cells cylindrical in shape and with their entrances oriented vertically downward. The presence of combs must be inferred as the primitive condition in the subfamily, since it occurs in other social wasps and all genera of hover wasps except *Metischnogaster*, even in astelocytarus nests. The cells may be rather scattered in a species of *Liostenogaster* and one of *Parischnogaster* which build the nest directly on the substrate, but this cannot parsimoniously be considered as primitive. The arrangement in vertical series is found in *Parischnogaster* and *Metischnogaster* (cf. figs. in Pagden, 1962; Yoshikawa et al., 1969; Ohgushi et al., 1983c), but the form varies within *Parischnogaster*, with comblike arrangements common in *P. mellyi* (cf. pl. II, fig. 1f of Vol. 2 of Saussure, 1852–1858). Hansell (1981) showed that this species was capable of building a range of designs, including linear arrangements, and other species construct “intermediate” nests of elongated combs (figs. in Iwata, 1967; Yoshikawa et al., 1969; Ohgushi et al., 1983c; Ohgushi and Yamane, 1983). *Holischnogaster* also builds an elongate, excentrically attached comb (Hansell, 1986b), and *Anischnogaster* nests encompass a similar range of variation, with a vertical series occurring in one species (van der Vecht, 1972: figs. 57–60). Nests of *Stenogaster* and *Eustenogaster* are different in that they are basically campanulate in form (cf. Pagden, 1958: figs. 4–9 with Spradbery, 1975: figs. 1–3). This latter design may be synapomorphic in these two genera, and elongated combs may similarly characterize *Anischnogaster* + (*Metischnogaster* + (*Holischnogaster* + *Parischnogaster*)), but the evolution of linear series within the latter group must entail some convergence. Hansell (1981) applied Jeanne’s (1975) suggestion that elongate linear nests are ad-

aptations for concealment from visual predators. For stenogastrines these would be vespines, but if so this "adaptation" has not been shown to be generally successful (cf. Williams, 1919; Hansell, 1982a; Turillazzi, 1985a for documentation of hornet predation on linear nests). In any event, the interpretation proposed here leaves open the question of whether the irregular comb characterizing *Liostenogaster* (in a general way) is primitive.

Pagden (1958) divided the Malayan species into three groups based in large part on nest architecture, corresponding to the genera *Eustenogaster*, *Liostenogaster* and *Parischnogaster*; *Metischnogaster* was possibly a fourth group. This scheme was elaborated by Ohgushi et al. (1983b: fig. I-4) into a detailed evolutionary scenario of nest architecture. The nest architecture of a putative species of *Liostenogaster* was treated as primitive, and adaptive changes from this were hypothesized to have been brought about by predation pressure. This led to the conclusion that where the nest architecture did not show comb formation it was secondary. This scenario shows general congruence to the present analysis, although the reservation must be expressed that simply because *Liostenogaster* is relatively plesiomorph in Figure 2, that does not mean that all of its traits are primitive. Ohgushi et al. also subdivided *Parischnogaster* into three species groups (*striatula*, *mellyi* and *jacobsoni*) and suggested transitions between architecture types among these groups. Evaluation of that aspect of their scenario must await phylogenetic analysis of the species of *Parischnogaster*.

29. Ant guards. The possible influence of predation on the evolution of nest shape was previously mentioned. Other specific features of nests may be attributed to protection from cursorial predators, namely ants. The disc-like structures on the supports of nests in several species, known as "ant guards," were suggested to provide protection from ants by Williams (1919). They are of two dissimilar types. Structures made of the same material as the rest of the nest are found in species of *Parischnogaster* and *Metischnogaster* (Pagden, 1958, 1962; C. K. Starr, pers. comm.). Secreted structures are found in other species of *Parischnogaster* (Turillazzi and Pardi, 1981; C. K. Starr, pers. comm.), as well as *Eustenogaster* (Pagden, 1958; fig. 8; C. K. Starr, pers. comm.) and possibly *Stenogaster fulgipennis* (van der Vecht, 1975). Turillazzi and Pardi (1981) confirmed that the ant guard material of *Parischnogaster nigricans serrei* repels a few species of ants, and that the material is secreted, at least for the most part, from the abdomen. However, the repellent effect was not universal. It appears that the different types of structures have arisen *de novo* on several occasions within the subfamily. Other forms of protection from ants found in other social wasps, such as the application of oral secretions and rubbing of the nest petiole with the terminal metasomal sterna (behavior patterns 8 and 9 of Sakagami and Yamane 1983: table I-2), evidently have no counterpart in stenogastrines. In that respect hover wasps are relatively primitive.

30. Envelope. Stenogastrine nests are typically gymnodomous, as is also true of nests of primitive paper wasps. However, nests of *Eustenogaster* are enclosed by an envelope. As pointed out by Iwata (1967), in most species the envelope is merely an elaboration of the outer walls of the peripheral cells, for which the term "pseudenvelope" has been used (Yoshikawa et al., 1969). Something approaching this is seen in a *Liostenogaster* species (Yoshikawa et al., 1969: figs. 5-6). However, in *E. calyptodoma* there is an envelope constructed independently of the comb, as is the case in higher social wasps. This last is clearly convergent, as it is within higher social

wasps; Polistinae do not primitively construct an envelope. Construction of an envelope is an autapomorphy of *Eustenogaster*, with the independent envelope found in *E. calyptodoma* perhaps derived from the "pseudenvelope" found in other species of the genus.

31. Oviposition. Oviposition behavior in Stenogastrinae has been described by Pardi and Turillazzi (1981), Hansell (1982a), Turillazzi and Pardi (1982), Sakagami and Yamane (1983) and Turillazzi (1985e). It is an indirect process. After placing a droplet of secretion from the metasoma in the mouthparts (not in the cell as stated by previous authors; Turillazzi, 1985e), the egg is extruded, grasped by adhering to the secretion in the mouthparts, and deposited in the cell. Further secretions from the metasoma are then placed upon the egg. As emphasized by all of these authors, this behavior is unique in the Vespidae. It is an autapomorphy, hence completely uninformative on relationships, and hence of no use whatsoever in analysis of interrelationships of Stenogastrinae and other vespid subfamilies, contrary to Sakagami and Yamane (1983) and Turillazzi (1985e).

32. Provisioning. As discussed previously, the provisioning of cells in Stenogastrinae shows derived similarity with Polistinae + Vespinae. It is simultaneous and progressive, and consists of a masticated arthropod paste. To the extent that sufficient food is provided for a day or more (Spradbery, 1975), hover wasps are primitive relative to other social wasps, and so "intermediate." The actual hunting itself was first described by Williams (1928). It involves hovering by the wasp at a spider's web and plucking of small prey from the web. This is characteristic and unique, hence an autapomorphy of the subfamily. Related issues are whether food is provided before egg hatch, and to what extent it is endogenous (of glandular origin). Spradbery (1975) and Sakagami and Yamane (1983) have considered provision before egg hatch to be a primitive feature similar to the state found in Eumeninae, and the latter authors argued that it showed phylogenetic relationship to Eumeninae, which is obviously a misinterpretation based on symplesiomorphy. But the whole character may be questioned. As discussed above under oviposition, what is provided before egg hatch is primarily a substance of glandular origin which may not have a trophic function (Hansell, 1982a; Turillazzi, 1985d). To the extent that prey items are ever provided prior to egg hatch (one species, Turillazzi, 1985d), they are malaxated or very small and incorporated into the secretion. The secretion has not been observed to have been consumed, and may instead serve a variety of other functions, including that of a platform for food (Turillazzi, 1985d). The use of the substance in itself is autapomorphic for the subfamily, as noted above. If in fact it does not have a trophic function, then stenogastrines show derived similarity to other social wasps in also not provisioning until after egg hatch.

33. Trophallaxis. Spradbery (1975) listed larval-adult trophallaxis as "probably not" occurring in Stenogastrinae, which is another symplesiomorphy with Eumeninae and so not informative on relationships. However, there is some doubt that this behavior is absent in Stenogastrinae (Turillazzi and Pardi, 1982; Turillazzi, 1985b, 1986a). It should be studied further; if the behavior is confirmed in hover wasps it might be another synapomorphy with other social wasps, although the behavior patterns would be rather different. Be that as it may, another form of trophallaxis, that between adults, probably is a synapomorphy of the social wasps. It has been reported in numerous studies of Stenogastrinae (Williams, 1928; Pagden, 1962; Tu-

rillazzi and Pardi, 1982; Hansell, 1983, 1987; Sakagami and Yamane, 1983; Turillazzi, 1985a, b, 1986b) and should be looked for in other species in order to assess its generality. It does not occur in solitary vespids, but is well known in other social vespids, and Pardi and Turillazzi (1982) cited it as a similarity between these three subfamilies, but then attributed it to convergence. As indicated by the results of Carpenter (1981) and in the section on subfamily placement, there is no evidence that the view of convergence is correct.

34. Thermoregulation. Rare wing fanning is the only putative thermoregulatory behavior known to occur in hover wasps (Williams, 1919; Sakagami and Yamane, 1983). Absence of such highly derived behaviors as transport of water droplets is simply primitive, but wing fanning, if general and indeed thermoregulatory, could be another derived similarity with other social wasps.

35. Extraction of meconium. This is part of the extended care, into the pupal stage of these wasps. First suggested by Spradbery (1975) for *Stenogaster concinna*, it has since been observed in other stenogastrines (Turillazzi and Pardi, 1981; Sakagami and Yamane, 1983; Turillazzi, 1986b). The meconium is extracted through the entrance to the cell. In those paper wasps which extract the meconium, it is done through the bottom of the cell (Jeanne, 1980) or after adult eclosion. This extraction behavior, if shown to be general in the subfamily, would be another autapomorphy. Turillazzi (1985b) suggested that the meconium is removed either for hygienic reasons or to facilitate the emergence of the adult, or both.

36. Closure. Sealing of the rearing cell "rarely" by the female in Stenogastrinae was a feature mentioned by Spradbery (1975); in Eumeninae the female always seals the cell (this is also true of other solitary vespids) but in higher social wasps the female does not do so. Sealing of the rearing cell is actually more common in the subfamily than stated by Spradbery. Complete sealing has been reported in *Liostenogaster varipicta* (Williams, 1919), *L. nitidipennis* (Iwata, 1967), *Anischnogaster iridipennis* (van der Vecht, 1972), *Parischnogaster timida* (Williams, 1919), *P. mellyi* (Iwata, 1967; Hansell, 1981), *P. nigricans serrei* (Iwata, 1967; Pardi and Turillazzi, 1981), and *Holischnogaster gracilipes* (Hansell, 1986b). Partial sealing of the rearing cell, which is no more than narrowing of the entrance, has been observed in *Parischnogaster depressigaster* (Williams, 1919), *P. striatula* (Iwata, 1967), *P. alternata* (Turillazzi, 1986b), *Eustenogaster calyptodoma* (Sakagami and Yoshikawa, 1968) and *E. eximia* (Krombein, 1976). Only *Stenogaster concinna* has been reported to provide no form of cell closure (Spradbery, 1975). The ground-plan state of Stenogastrinae is thus parsimoniously inferred to be sealing of the cell, given the cladogram of Figure 2. As such it is a symplesiomorphy, and so uninformative on subfamily relationships. Loss of this trait is perhaps another shared derived similarity between *Eustenogaster* and *Stenogaster*, but if so there is convergence in some species of *Parischnogaster*.

37. Cocoon. Spradbery (1975) noted that in Stenogastrinae the pupal cocoon was not complete, whereas in the other subfamilies he listed it was. *Parischnogaster depressigaster* (Williams, 1919), *Eustenogaster calyptodoma* (Sakagami and Yoshikawa, 1968), and *E. eximia* (Krombein, 1976) have been reported to line the cell wall with silk but not to have a complete cocoon. Other species appear to lack a cocoon entirely. An incomplete cocoon then, is the groundplan condition in the subfamily, an autapomorphy, and hence uninformative on subfamily relationships. It may be added that the suggestion of Iwata (1976) that sealing of the rearing cell

occurs because there is no cocoon spun is illogical; the first trait is primitive and the second is derived, and so they cannot be causally related.

38. Nest sharing. As discussed previously, on present evidence nest sharing is parsimoniously inferred to be a synapomorphy of the three social wasp subfamilies. It may characterize the colony cycle in all species of hover wasps, but is possibly only facultative; long-term observation on many species is required to establish this. Colony foundation is by single foundresses in Stenogastrinae, although absconding swarms (West-Eberhard, 1982) have been observed (Turillazzi, 1985a). Recruitment usually occurs by addition of daughters (Krombein, 1976; Turillazzi, 1982, 1985a; Hansell, 1983, 1987; Yamane et al., 1983a; inferred by van der Vecht, 1972, and Spradbery, 1975). Recruitment by joining has also been reported in *Liostenogaster flavolineata* (Hansell et al., 1982), *P. nigricans serrei* (Turillazzi, 1982, 1985a), *P. mellyi* (Hansell, 1983; Sakagami and Yamane, 1983), and *P. alternata* (Turillazzi, 1985c). Joining typically occurs prior to the emergence of brood and is frequently accompanied by usurpation or is short-term (Turillazzi, 1982, 1985a; Hansell, 1983, 1987; Sakagami and Yamane, 1983; Yamane et al., 1983a). Joining may occur later in the colony cycle (Yamane et al., 1983a) or persist for a relatively extended time (Turillazzi, 1985c, 1986a, b) but seems to me qualitatively similar in all these cases, contrary to Turillazzi (1985c, 1986a, b). An apparently different phenomenon is the internidal drifting first reported for *P. striatula* (Yoshikawa et al., 1969). In a small aggregation of very closely spaced colonies they observed frequent movement of marked females among several nests. However, Hansell (1982b) repeated this study and did not find frequent interchange, but instead active nest defense against conspecifics. Females only succeeded in landing on foreign nests when no resident was there and then attacked the brood. As Hansell pointed out, the data published by Yoshikawa et al. (1969) do not indicate whether females landed on nests in the presence of a resident. Similar comments apply to the internidal drifting reported in *P. mellyi* by Yamane et al. (1983a, b). The interchange apparently occurred on abandoned or usurped nests, which would accord with the observations of Hansell (1981, 1983) of typical active nest defense in this species. Remarkably, Yamane et al. (1983a, b) stated that reoccupants and usurpers continued to rear the brood of the previous occupant, although they also stated (1983a:21) "it is uncertain whether there occurred any selective eating or elimination by new occupants." Hansell (1987) has reported similar rearing of brood by usurpers in *Eustenogaster calyptodoma*, and suggested that acquisition of a brood is advantageous in providing (eventual) foraging assistance. Frequent interchange among closely spaced colonies may thus be usurpation attempts, and joining explicable if average relatedness was high or mutual care of the nest occurred—and moving females had a sufficient chance of reproduction on the new nests (Yamane et al., 1983a). Shifts between (young) nests are well known in *Polistes* (West-Eberhard, 1969; Kasuya, 1981; Itô, 1984) and are generally considered to be among closely related individuals (e.g., Ross and Gamboa, 1981).

Cell re-use during a single colony cycle may also be general in the subfamily; it is usually noted in long-term studies (nest re-use has also been reported: Yamane et al., 1983a; Turillazzi, 1985a). If cell re-use is general, it is another synapomorphy with other social wasps.

39. Division of labor. Cooperative brood care was reported in *Parischnogaster depressigaster* and *Liostenogaster varipicta* by Williams (1919) in the first behavioral

study of hover wasps. It has since been observed in every long-term study. Division of labor has also been observed. A linear dominance hierarchy has been reported in *Parischnogaster* sp. (Yoshikawa et al., 1969) and *P. nigricans serrei* (Pardi and Turillazzi, 1981; Turillazzi and Pardi, 1982). A three-level dominance hierarchy has been observed in *Liostenogaster flavolineata* (Hansell et al., 1982). Position in the hierarchy is correlated with ovarian development. Division of labor occurs in *P. mellyi* (Hansell, 1983; Yamane et al., 1983a, b), *Holischnogaster gracilipes* (Hansell, 1986a), *Eustenogaster eximia* (Krombein, 1976) and *E. calyptodoma* (Hansell, 1987), but clear dominance hierarchies have not been identified. Rather, certain individuals spent more time on the nest while others spent more time foraging, and this was correlated with ovarian development. The workerlike individuals may be daughters of the foundress (Krombein, 1976; Yamane et al., 1983a; Hansell, 1987). All females may eventually mate (Turillazzi, 1985a, 1986a, Hansell, 1987), subordinates are presumed to lay eggs (Hansell, 1983), and subordinates have been observed to become foundresses (Turillazzi, 1982; Yamane et al., 1983a, b) or come to dominate (Hansell et al., 1982). Turillazzi and Pardi (1982) reported statistical size differences correlated with fertilization in *P. nigricans serrei*, but Turillazzi (1985a) did not find any in the same species. Similar variation in the statistical differences reported by Richards and Richards (1951) for some paper wasp species has been observed (Carpenter and Ross, 1984). Therefore morphological castes apparently do not exist in Stenogastrinae. Instead, these reports indicate that the reproductive division of labor is behavioral—and temporal. Workerlike behavior may be an alternative reproductive strategy (West-Eberhard, 1981) whose expression is facultative (West-Eberhard, 1987) and often temporary.

All of these species are at stage III, the “rudimentary-caste-containing stage,” of West-Eberhard’s (1978) model for the origin of social behavior in wasps, as realized by Hansell (1983) and Turillazzi (1985a). The question is then whether temporary division of labor also characterizes all those species where nest sharing occurs in smaller colonies or persists over a relatively shorter part of the colony cycle. It was not observed in *Stenogaster concinna* by Spradbery (1975), but he apparently did not make detailed observations on the multi-female nests he found. It has been reported in the small, short-term colonies of *Eustenogaster* (Krombein, 1976; Hansell, 1987), where daughters assist their mothers in brood care. Critical study of other species, particularly in these two genera and *Anischnogaster*, is required to establish the generality of temporary division of labor, but it may occur in all stenogastrine species. If this is true it is another synapomorphy of all social wasps, rather than just Polistinae + Vespinae (Carpenter, 1981). This would have two major implications. First, the groundplan condition in Stenogastrinae would then differ little from the ancestral condition in Polistinae—only in the presence of permanent sterility in the latter group. And here it should be recalled that the workers in the primitive paper wasp genera are at least initially “hopeful” reproductives (West-Eberhard, 1978) and worker behavior thus in a sense conditional (West-Eberhard, 1981). Mechanisms for queen control (monopolization of oviposition, West-Eberhard, 1987) are better developed in Polistinae than Stenogastrinae. Second, the distinction between West-Eberhard’s (1978) “primitively social stage (II)” (casteless nest sharing) and “rudimentary-caste-containing stage (III)” is then not exemplified in the social Vespidae

clade, and so the distinction has perhaps not been important in the evolution of this group.

40. Male behavior. The mating systems of very few hover wasps have been studied. Primarily unisexual aggregations away from nests—"male clubs" (Hansell, 1986a) have been reported in *Eustenogaster luzonensis* (Williams, 1919), *Stenogaster concinna* and *Anischnogaster iridipennis* (Spradbery, 1975), *Parischnogaster mellyi* (Turillazzi, 1983a), and *Holischnogaster gracilipes* (Hansell, 1986a). It is unknown whether this behavior functions in reproduction. Patrolling and displaying behavior away from nests has been observed in *Metischnogaster* (Pagden, 1958, 1962), *Parischnogaster nigricans serrei* and *mellyi* (Turillazzi, 1982, 1983a, b), and *Liostenogaster* (Turillazzi, 1986a); marking of perches occurs in the latter. Switching between aggregations and patrolling at particular times of day occurs in *P. mellyi* (Turillazzi, 1983a). Male behavior is quite diverse in Eumeninae (cf. Smith and Alcock, 1980), and although patrolling is common in Polistinae, it is not in *Polistes* (cf. Jeanne and Castellón Bermúdez, 1980). Patrolling in loose aggregations is typical in Vespinae (e.g., Post, 1980), although sibling mating on the natal nest may be common (e.g., Akre et al., 1982). Given the few data on hover wasps and this diversity in the outgroups, it does not seem possible to specify the direction of evolutionary change at this time.

RESULTS

The cladogram for the characters coded in Table 2 is shown in Figure 2. The length of the cladogram is 16. The consistency index (the sum of the states of all the characters, divided by the length of the tree; Kluge and Farris, 1969) is 0.875. The matrix of Table 2 includes three autapomorphic states; when these are deleted the length of the cladogram is 13, with a consistency index of 0.846. The characters are highly congruent; only two extra steps are required. These are in character 5, the number of male mandibular teeth, and character 16, the propodeal sculpture. Convergence is thus inferred for both of these characters. The other characters listed in Table 2 support the cladogram quite strongly. The diagnosis of the cladogram (Farris, 1979) for all of the characters discussed in this paper follows: the synapomorphies of each grouping of genera and autapomorphies of each genus are summarized. Apomorphic groundplan features of the subfamily as a whole are also listed.

STENOGASTRINAE

Autapomorphies not discussed by Carpenter (1981) include: character 1, forewing second submarginal cell rectangular; 6, labial palpus with first segment greater than or approximately equal to the combined length of segments 2–4; 10, pronotal and pretegular carinae lost; 21, male sternum VII flattened; 25, larva with antennal papilla; 26, larval mandible with one tooth set back from margin; 31, indirect oviposition; 32, hunting behavior and use of endogenous substance as food platform; 35, meconium extraction; 36, pupal cocoon incomplete. The following apomorphic behavioral characters are interpreted as synapomorphies with Polistinae + Vespinae: 27, nests constructed with plant material (?); 28, nests free hanging; 32, simultaneous progressive provisioning with masticated arthropod paste, after egg hatch (latter

Table 2. Character codings for each genus.

<i>Liostenogaster</i> SMOOTH	NORMAL	GAP SPINOSE	POINT NORMAL	THREE	EQUAL	NORMAL	ROUND
<i>Parischnogaster</i> STRIATE	PETIOLE	FUSED FLAT	POINT DILATED	THREE	EQUAL	CLUB	NARROW
<i>Holischnogaster</i> STRIATE	PETIOLE	FUSED FLAT	POINT DILATED	THREE	EQUAL	CLUB	NARROW
<i>Metischnogaster</i> STRIATE	PETIOLE	FUSED SPINOSE	POINT DILATED	TWO	EQUAL	FLAT	NARROW
<i>Anischnogaster</i> PUNCTATE	PETIOLE	FUSED SPINOSE	POINT NORMAL	THREE	EQUAL	NORMAL	ROUND
<i>Stenogaster</i> STRIATE	NORMAL	FUSED SPINOSE	ROUND NORMAL	ONE	GREATER	TIPPED	ROUND
<i>Eustenogaster</i> SMOOTH	NORMAL	FUSED SPINOSE	ROUND NORMAL	ONE	GREATER	NORMAL	ROUND

aspect only probable); 33, adult trophallaxis, possibly also larval-adult trophallaxis; 34, thermoregulation by wing fanning (?); 38, nest sharing and cell re-use; 39, cooperative brood care and temporal division of labor (probable). The groundplan condition of character 40, male behavior, is unclear.

Liostenogaster

The only autapomorphy of this genus is character 16, propodeum smooth, which is convergent in *Eustenogaster*.

(*Eustenogaster* + *Stenogaster*) + (*Anischnogaster* + (*Metischnogaster* + (*Holischnogaster* + *Parischnogaster*)))

The grouping of all hover wasp genera aside from *Liostenogaster* is supported by character 3, fusion of the occipital carina with the hypostomal carina.

Eustenogaster + *Stenogaster*

A sister-group relationship between these two genera is supported by three morphological characters: 4, male clypeus rounded ventrally; 5, male mandibular teeth reduced to one; and 7, maxillary palpus with the length of segment 2 greater than the combined length of segments 3–6. Two behavioral features may also support this relationship: 28, nests campanulate in shape; and possibly 36, cells not completely closed by female. Character 6, first segment of labial palpus relatively longer than in other hover wasps, may also be a shared derived feature of these genera.

Eustenogaster

Autapomorphies of the genus include: 2, pigmented posterobasal area in male hindwing; 13, scutellum strongly carinate; 16, propodeum smooth (convergent in *Liostenogaster*); 30, nest with "pseudenvelope."

Stenogaster

The monophyly of this genus is shown by characters 8, male antenna with apical flagellomere modified; 15, raised lamella above propodeal orifice; 23, volsella with cusps + lamina strongly narrowed medially.

Anischnogaster + (*Metischnogaster* + (*Holischnogaster* + *Parischnogaster*))

The grouping of these four genera is supported by character 20, development of a petiole on metasomal segment II. Character 28, nest with comb elongated, may also support this component.

Anischnogaster

The monophyly of this genus is weakly established by character 5, male mandible with proximal teeth blunted; and 16, propodeum punctate (polarity unclear).

Metischnogaster + (*Holischnogaster* + *Parischnogaster*)

The grouping of these three genera is supported by character 14, narrowing of the propodeal valvula posteriorly; and 24, aedeagus apically compressed and dilated in lateral view.

Metischnogaster

The monophyly of *Metischnogaster* is shown by a large suite of features, including characters 2, hindwing with posterior fringe of hairs greatly elongated; 5, male mandible bidentate; 8, male antenna with flagellomeres flattened; 9, vertex with median longitudinal groove; 11, notauli strongly impressed; 12, male pleural area sunken, densely pubescent, and bordered posteriorly by carina; 14, propodeal valvula essentially lost; 17, male foretibia with spatulate setae; 19, spiracles of metasomal segment II visible in dorsal view; 24, aedeagus with subapical lateral projections; 29, nest with ant guards.

Holischnogaster + *Parischnogaster*

A sister-group relationship between these two genera is established by two features: 8, distally swollen antennae; and 22, male parameral spine flattened and greatly enlarged.

Holischnogaster

This genus is certainly monophyletic, since it is monotypic. However, it does not have any autapomorphies among the characters discussed in this paper. Of the two features by which it was distinguished from *Parischnogaster* in the original description (van der Vecht, 1977a), male midtarsi symmetrical and mouthparts elongate, it has the plesiomorphic state in the first and possibly the second as well (see above). As discussed below, recognition of a separate genus for this species seems unjustified.

Parischnogaster

The monophyly of this genus is shown by character 18, male midtarsi asymmetrical. The mouthparts of *Parischnogaster*, specifically the palpi, tend to be shorter than in its sister-group, but there is variation within the genus (as well as among other stenogastrines), and in my view the differences between the two genera are not significant.

DISCUSSION

The implications of the results of this analysis are of three sorts. The first is taxonomic. All of the previously recognized genera are monophyletic—but that does not mean that recognition of all of them is well justified. *Holischnogaster* is differentiated from its sister-group *Parischnogaster* primarily by plesiomorphy in one character. Although a sister-group relationship is thereby formally recognized, little is gained in the process of efficient description of character data (diagnostic efficiency of Farris, 1979) which is the purpose of classification. Recognition of *Holischnogaster* itself contributes nothing to this process, and separation of *Parischnogaster* contrib-

utes only one character, male midtarsi, which varies within other vespid genera. By contrast, one of the characters establishing this sister-group relationship, parameral spine dilated, is an outstanding feature, unique in the entire family. Van der Vecht (1977a:73) separated *Holischnogaster* as a genus because "there may be important differences in behaviour with regard to feeding and mating." No differences have yet been shown, and in any event the similarity in the male genitalia seems far more "important" as a genus character. The recognition of two genera in this case is just the sort of oversplitting which has rendered the classification of other vespid subfamilies chaotic, with an inflexible, confusing nomenclature and little discernible benefit (cf. Carpenter and Cumming, 1985; Carpenter, 1986, 1987). As I have done in Vespinae (Carpenter, 1987), I am resisting this trend here. *Holischnogaster* is here-with synonymized with *Parischnogaster* (NEW SYNONYMY).

The second implication of the results concerns biogeography. The Stenogastrinae are endemic to the Indo-Pacific, ranging from the Indian subcontinent and Sri Lanka to New Guinea. Two genera, *Stenogaster* and *Anischnogaster*, are endemic to New Guinea and neighboring islands (Waigeo, Misool, Aru, Yapen; cf. van der Vecht, 1972, 1975). This type of distribution has been termed Papuan (e.g., Gressitt, 1956), and was classically considered to be a part of the Australian region (Wallace, 1860). The other genera do not occur any further east than Mindanao and Sulawesi (cf. Schulthess, 1927). Thus, their distribution is in the classical Oriental Region (Wallace, 1860). Replacing the taxa in Figure 2 with these areas, it is seen that the transition between the Papuan and Oriental Regions is replicated. This division corresponds to Wallace's famous line, and it might be thought that this accords with the classical treatment. However, two-area statements are basically uninformative in historical biogeography; the interesting question is what are the relationships of these two areas to a third. One potentially fruitful approach to this problem will be the study of the interrelationships of the species inhabiting the Oriental "region." Schuh and Stone-dahl (1986) cite evidence from several groups which shows that part of the Oriental "region" is more closely related to the Papuan "region" than to other parts of the Oriental "region." The same pattern may occur within the Oriental hover wasp genera.

Finally, there are various implications of this analysis for the evolutionary study of behavior. As discussed above, there is considerable evidence from behavioral data to support the close relationship of Stenogastrinae to Polistinae + Vespinae. The characters in the subfamily tables of Spradbery (1975) and Sakagami and Yamane (1983) show similarity in derived features between these groups. The characters where stenogastrines lack the derived states of other social wasps are either primitive absences or unique derived features in Stenogastrinae. There are thus no grounds for attributing similarity in the basic (groundplan) behavioral patterns in stenogastrines and other social wasps to convergence. Instead, such similarities must be inferred to be the product of descent from a common ancestor.

As the discussion of various aspects of social behavior shows, the hover wasps as a whole may not be very different in these aspects from the relatively primitive Polistinae. Stenogastrinae may primitively be at the rudimentary-caste-containing stage (III) of West-Eberhard's (1978) model for the origin of social behavior in wasps. This would indicate that the common ancestor of all social wasps attained this condition before diversifying, and so that the transition between West-Eberhard's

stage II (casteless nest sharing) is not exemplified within any subfamily—or that the distinction is not significant in Vespidae. However, the fundamental tenet of West Eberhard's model, that the evolution of eusociality occurred in polygynous family groups, is still corroborated by this inferred common ancestor. The basic (ancestral) differences between the social behavior in stenogastrines and that of the higher social wasps may then turn out to be: 1) dominance is more strongly enforced in the latter group (i.e., mechanisms of queen control are better), and 2) colonies are also larger. Dominance hierarchies have evolved convergently within Stenogastrinae and other social wasps, and doubtless other features of social behavior as well, but apparently eusociality as such is not convergent—although that term is applied in this case to a temporal, facultative phenomenon (a “serial polygyny”). The larger colonies of Polistinae + Vespinae have been attributed to beginning the nest with a petiolate cell (van der Vecht, 1977b), which Hansell (1985) speculated led to the selection of tough paper, thus permitting evolution of large nests. Is this relatively simple trait then the crucial difference between the hover wasp lineage with some 67 species (van der Vecht, 1977a), rather uniform in morphology, behavior and ecology, and the paper wasp–hornet lineage with over 800 highly diverse species?

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APPENDIX

List of taxa examined. N.C. indicates new combination. * indicates that the male genitalia were dissected.

Liostenogaster

- flavolineata* (Cameron)
nitidipennis (Saussure)*
varipicta (Rohwer), N.C.*
 1 new species*

Stenogaster

- adusta* Vecht*
concinna Vecht*
macilenta Vecht
Eustenogaster agilis (Smith), N.C.*

calyptodoma (Sakagami & Yoshikawa)*
eximia (Bingham)*
fulvipennis (Cameron), N.C.*
hauxwellii (Bingham)*
luzonensis (Rohwer), N.C.*
micans (Saussure)*
scitula (Bingham)*
3 new speices
Anischnogaster
dubia Vecht*
iridipennis (Smith)*
loriai maculata Vecht*
spilaspis (Cameron)*

Metischnogaster
cilipennis (Smith)*
drawseni (Saussure)*
Parischnogaster
depressigaster (Rohwer)*
gracilipes (Vecht), N.C.*
jacobsoni (Buysson)*
mellyi (Saussure)*
nigricans (Cameron)*
striatula (Buysson)
timida (Williams)